

Sex Differences in the Responses of the Human Amygdala

STEPHAN HAMANN

Department of Psychology, Emory University, Atlanta, Georgia

The amygdala is a structure in the temporal lobe that has long been known to play a key role in emotional responses and emotional memory in both humans and nonhuman animals. Growing evidence from recent neuroimaging studies points to a new, expanded role for the amygdala as a critical structure that mediates sex differences in emotional memory and sexual responses. This review highlights current findings from studies of sex differences in human amygdala response during emotion-related activities, such as formation of emotional memories and sexual behavior, and considers how these findings contribute to the understanding of behavioral differences between men and women. Clinical implications for the understanding of sex differences in the prevalence of affective and anxiety disorders are discussed, and future directions in the study of the amygdala's role in human sex differences are outlined. *NEUROSCIENTIST* 11(4):288–293, 2005. DOI: 10.1177/1073858404271981

KEY WORDS *Amygdala, Sex, Memory, Emotion*

The amygdala is a small, almond-shaped subcortical structure located in the temporal lobe that plays a key role in emotional memory and emotional responses in both humans and nonhuman animals (Fig. 1). The amygdala's neural connections to the rest of the brain put it in a unique position to rapidly respond to sensory input and influence physiological and behavioral responses, as well as to influence memory storage in the adjacent hippocampus. The classic view of the amygdala's role in emotion portrays this structure as being primarily involved in aversive, negative emotional states such as fear (Adolphs and others 1995; Calder and others 2001; Davis and Whalen 2001), but more recent studies have demonstrated that the amygdala's response to emotional stimuli is more general and that it responds primarily to the strength or intensity of a pleasant or unpleasant stimulus (Hamann and others 1999; Davis and Whalen 2001; Hamann and others 2002).

Psychological studies have identified a variety of sex differences in emotion-related behavior in humans. For example, women on average retain stronger and more vivid memories for emotional events than men (Seidlitz and Diener 1998; Canli and others 2002). Another prominent human sex difference is the substantially greater role that visual stimuli play in male sexual behavior. Recent neuroimaging studies using positron

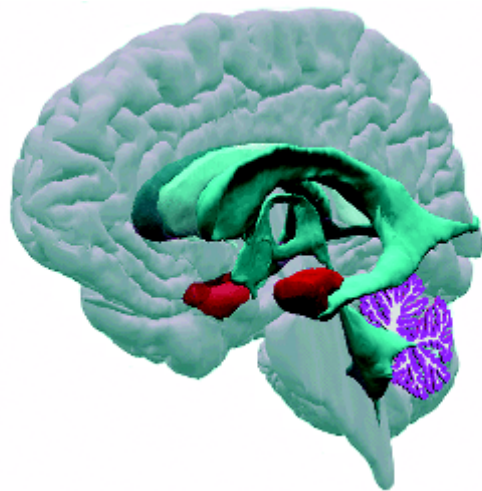


Fig. 1. The amygdala (red region), a small almond-shaped structure located deep in the anterior temporal lobe, plays a critical role in a variety of emotional processes including emotional memory and adaptive responses to emotional stimuli. Recent work suggests that several differences between men and women in emotional responses arise in part from sex differences in amygdala responses. Reprinted with permission by Digital Anatomist Project, Department of Biological Structure, University of Washington.

emission tomography (PET) and functional MRI (fMRI) have revealed that these and other sex differences in emotional responses are closely linked to differences in amygdala response. In this article, we address these and other recent findings that highlight an emerging new role for the amygdala as a key structure that mediates differences in emotional and sexual responses between men and women. These sex differences in the amygdala's

Grant support: This work was supported by the Center for Behavioral Neuroscience, a Science and Technology Center Program of the National Science Foundation, under agreement IBN-9876754 and NIH grant 1R24MH067314. The author thanks Kim Wallen, Rebecca Herman, and Carla Harenski for their significant contribution to this research.

Address correspondence to: Stephan Hamann, Department of Psychology, 532 North Kilgo Circle, Emory University, Atlanta, GA 30322 (e-mail: shamann@emory.edu).

Box 1: Structural and Functional Sex Differences in the Amygdala

In addition to functional differences in amygdala response, such as in emotional memory and in responses to sexually arousing stimuli, the amygdala in men and women differs in terms of structure and in aspects of brain development. These structural and developmental differences likely contribute to the functional differences observed in neuroimaging studies.

One major difference between the sexes is the size of the amygdala. In the adult human brain, the male amygdala is significantly larger than the female amygdala, even when total brain size is taken into account (Goldstein and others 2001). Although the specific consequences of this sex difference in amygdala size are not known, structural differences in brain anatomy often are associated with differences in brain function and response. For example, one recent study found a relation between the size of the amygdala in patients with epilepsy and sexual drive; patients with greater residual amygdala size after undergoing neurosurgery reported greater sexual drive and motivation (Baird and others 2004). Interestingly, the brain

regions that differ in size between men and women tend also to be the same regions that contain high concentrations of sex hormone receptors, suggesting that male and female hormones play a role in determining the size of specific brain regions such as the amygdala during brain development (Goldstein and others 2001). Consistent with this idea, neuroimaging studies have found that amygdala, which contains relatively high concentrations of sex hormone receptors, develops structurally at different rates in human males and females. Other structural differences in areas that receive strong neuronal connections from the amygdala, such as the hypothalamus, which is larger in men than women, may also contribute to sex differences in brain response that involve the amygdala. Circulating levels of sex hormones in the bloodstream constitute an additional influence on amygdala response through their action on receptor sites. Future work will be necessary to elucidate the complex relationship between structural, developmental, and functional aspects of amygdala sex differences.

function may be related to the structural and developmental sex differences that have been found previously for this structure, such as the high concentration of sex hormone receptors and the larger size of the amygdala in men than women (Newman 1999) (see Box 1).

The Amygdala and Sex Differences in Emotional Memory

Memory for emotional events is generally better than memory for emotionally neutral events (Hamann 2001). Several psychological studies have reported that men and women differ substantially with respect to emotional memory (Hamann and Canli 2004). For example, women can recall emotional memories more quickly, can recall more emotional memories in a given period of time, and report that the emotional memories they recall are richer, more vivid, and more intense. In general, then, women tend to experience greater enhancement of their memory by emotion (Seidlitz and Diener 1998). The stronger effect of emotion on women's memories is not entirely beneficial, however. As described below, emotion can also impair memory in some situations, and this impairment is accentuated in women. In addition, the fact that emotional memories tend to be stronger for women may be linked to the greater prevalence of depression and some types of anxiety disorders in women (Davidson and others 2002).

The three neuroimaging studies that have examined the brain correlates of these differences in emotional memories have found a remarkably consistent pattern of sex differences in the role of the left and right amygdala in emotional memory. These studies have focused on the

effects of emotional arousal on declarative memory, memory for facts or events that can be brought to mind through a conscious, voluntary effort to retrieve the memory (Squire and Zola 1996). Each of these studies examined differences in brain activity occurring during memory encoding (i.e., memory formation) that were predictive of subsequent successful emotional memory retrieval. That is, one can examine which items are successfully retrieved on a later test and then go back to determine which brain areas were more active when those items were originally encoded in the brain scanner.

Cahill and others (2001) used PET to image brain activity while men and women watched either highly aversive films or neutral films. The level of amygdala activity at encoding predicted later emotional memory performance for both males and females. However, for females, this relation was found in the left amygdala whereas for males it was in the right amygdala. A later study by Canli and others (2002) examined brain activity in men and women during the encoding of emotional and neutral scenes in photographs, using fMRI. Consistent with the prior PET study, amygdala activity during the encoding of the most emotionally arousing photographs was strongly related to later recognition memory for the emotional pictures, but again this relationship was seen in the left amygdala for women and the right amygdala for men. The strength of an emotional experience, referred to as emotional arousal, is currently thought to be the most important factor that determines the degree of memory enhancement associated with an emotional event (Hamann and others 1999; Canli and others 2000). In this study, participants' rat-

ings of emotional arousal correlated with left amygdala activity in both men and women. Thus, in females the brain regions involved in emotional reactions coincide with those involved in encoding memory for the experience, whereas in males these processes occur in different hemispheres. The authors suggested the greater overlap between the neural correlates of emotional experience and emotional memory in women as a possible explanation for the greater vividness and accuracy of their emotional memories.

In the third study, Cahill and others (2004) examined memory for emotionally arousing photographs in men and women using a similar fMRI task as was used by Canli and others (2002) and again found that later levels of emotional memory were strongly correlated with left amygdala activity in women but right amygdala activity in men. In summary, these studies have found a consistent sex difference between the role of the left and right amygdalas (Fig. 2). Speculations regarding the origin of these sex differences have included sexually dimorphic brain development (Goldstein and others 2001), the influence of sex hormones both during development and during adulthood, and possible differences in the cognitive style used by men and women in encoding emotional experiences.

Strange and others (2003) examined the effect of inserting an emotional event (an emotionally arousing word) into a sequence of neutral events (a list of neutral words). As expected, memory for the arousing word was better than memory for the neutral words. Interestingly, however, memory for words presented just before the emotional word was also affected, but instead of enhancement, memory was impaired. This impairment was not found in a patient with bilateral amygdala lesions, strongly suggesting that the effect is amygdala-dependent. In addition, the size of the emotion-induced memory impairment was found to be twice as large for women than for men. The specific mechanisms responsible for this memory impairment are yet unknown, but these findings are noteworthy in that they suggest that both the enhancing and the impairing effects of emotion are magnified in women.

Sex Differences in Amygdala Response to Sexual Stimuli

The amygdala has long been known to play a role in sexual behavior, from the results of animal studies as well as clinical evidence in humans linking temporal lobe seizures located near the amygdala to sexual behavior such as sexual automatisms (Leutmezer and others 1999). Bilateral damage to the amygdala and surrounding cortical areas results in the so-called Klüver-Bucy syndrome in monkeys (and, more rarely, in humans), characterized by atypical and indiscriminate sexual behavior.

Studies with rats with amygdala lesions have highlighted a key distinction between the role of the male amygdala in so-called appetitive and consummatory sexual behaviors. Appetitive sexual behaviors involve moti-

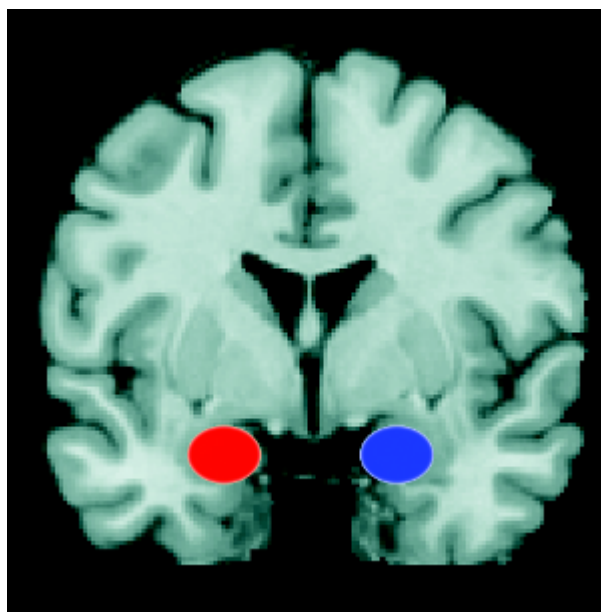


Fig. 2. The left and right amygdala have different roles in the encoding of emotional memory for events for men and women. The left amygdala (red oval) and right amygdala (blue oval) are shown on a coronal MRI slice through the center of the amygdala. For women, the level of activity in the left amygdala recorded using PET or fMRI during an emotional event correlates strongly with the probability that the event will be remembered on a later memory test, whereas activity in the right amygdala is not related to subsequent memory performance. Conversely, for men, activity in the right amygdala (but not left amygdala) during an emotional event correlates strongly with later memory for the event. The strength of emotion experienced during an event correlates with left amygdala activity in both men and women, however, indicating that in females the brain regions involved in emotional reactions coincide with those involved in encoding memory for the experience, whereas in men these processes occur in different hemispheres. The greater overlap between the neural correlates of emotional experience and emotional memory in women may help account for the greater vividness and accuracy of their emotional memories.

vation to obtain a sexual reward (i.e., desire or wanting), whereas consummatory sexual behaviors involve obtaining a reward (i.e., copulation). Everitt (1990) reported that lesions to the medial amygdala impaired the ability of male rats to respond to olfactory and other sexual cues from a receptive female, implicating this structure in appetitive sexual motivation. Male rats were trained to gain access to receptive female rats that were placed above them in a plastic enclosure by repeatedly pushing a lever that would open a trapdoor. Amygdala lesions markedly reduced bar-pressing behavior to obtain females but did not interfere with sexual behavior when the females were placed next to the males. Because lesions to the medial amygdala do not affect female sexual receptivity, this demonstrated that in rats the amygdala is critical for male but not female appetitive sexual responses.

Moving to studies of humans, researchers have drawn on these previous animal findings to guide their search for brain regions that may differ between men and

women in the domain of sexual behavior. These studies have used neuroimaging to examine the brain basis underlying a major sex difference in responses to appetitive visual sexual stimuli, namely, the greater male response to such stimuli. Numerous studies have demonstrated that men are more psychologically and physiologically responsive to visual sexually arousing stimuli and display a greater motivation to seek out and interact with such stimuli (Symons 1979). This specific sex difference is predicted by evolutionary and sociobiological theories that postulate that it is adaptive for males to react rapidly to visual information that signals an opportunity to mate with a fertile female because this tends to increase their probability of passing on their genes. Because of the greater maternal investment in time and resources for childrearing, a similar rapid arousal response to visual stimuli is not adaptive for females.

We recently conducted an fMRI study investigating this issue (Hamann and others 2004). Of particular interest was whether men and women would differ in activity in the amygdala and hypothalamus, based both on prior converging evidence from animal studies and the key role of the amygdala in mediating emotional responses. We tested two leading hypotheses concerning how sex differences in activations to sexual stimuli might arise. If men exhibit greater brain activations than women in response to visual sexual stimuli, this neural difference may arise simply because the men typically respond with greater psychological and physiological arousal rather than because of any sex difference per se. In contrast, the processing mode hypothesis proposes that sex differences in brain activation elicited by sexual stimuli arise from differences in cognitive styles or neural pathways recruited by men and women during the processing of sexual stimuli, not from arousal. By this view, men and women should differ in their neural responses to sexual stimuli even after they have been matched on arousal.

Thus, the goal was to test these hypotheses by comparing men and women on their responses to visual sexual stimuli under conditions in which they were equated on elicited arousal. Matching the sexes on arousal required careful preselection of visual sexual stimuli. We examined brain activity with fMRI in 14 men and 14 women while they viewed sexually arousing photographs, neutral photographs, or a control condition in which a blank screen with a visual fixation cross (+) was presented. Ratings of sexual arousal were also assessed, and these confirmed that men and women were successfully equated on arousal.

The primary finding was that the amygdala and hypothalamus exhibited substantially more activation in men than in women when viewing the same sexually arousing visual stimuli. This can be seen in Figure 3*a*, which shows the regions where men showed significantly greater activation than women for the sexual stimuli compared to the fixation control, especially in the left amygdala. The separate group brain activation maps of the same comparison for men and women are shown in

Figure 3*b* and 3*c*, respectively. In contrast to men, there was a lack of significant activity in the bilateral amygdala and the hypothalamus for women in response to sexually arousing photographs (Fig. 3*c*). When we contrasted the activations for the sexually arousing stimuli with the closely matched nonsexual neutral stimuli, which controlled for the presence of pleasant social stimuli and faces, we obtained similar results. Remarkably, no areas of greater activation for women than for men were found. Another fMRI study, conducted by Karama and others (2002), also examined sex differences in brain responses to sexually arousing visual stimuli (films). Greater activity for men in the hypothalamus (which receives substantial amygdala output) was observed, consistent with our results, but greater activity in the amygdala itself was not found. However, these authors have recently conducted a follow-up study using shorter versions of their film stimuli (a design more sensitive to rapid changes in amygdala activity) and have obtained preliminary results that replicated our finding of greater left amygdala activity in men (S. Karama, personal communication, August 2004).

Overall, the results of our study favor the processing mode hypothesis rather than the arousal hypothesis because they were obtained when arousal had been equated for men and women. The greater amygdala activation for men is particularly interesting because this sex difference parallels the findings of prior studies with rats implicating the amygdala in male sexual motivation. A motivation interpretation would also be consistent with neuroimaging studies that have strongly implicated the human amygdala in other forms of appetitive motivation, for example, desire for food or drugs (Arana and others 2003; Gottfried and others 2003). By this view, the greater amygdala activation for men reflects a greater appetitive motivation or desire elicited by visual sexual stimuli. If this view is correct, then future neuroimaging studies that assess appetitive motivation, for example, by requiring subjects to expend money or effort to view sexual stimuli, should find a strong relation between this measure of motivation and amygdala activity.

Another intriguing human parallel with the differential roles of the amygdala in male appetitive (precopulatory) versus consummatory (copulatory) sexual responses demonstrated in rats was found in a PET study of brain activity in men during consummatory sexual behavior (Holstege and others 2003). Relative to rest, consummatory male sexual behavior (orgasm) elicited decreased activity in only one area, the left amygdala. Similar decreases were not reported for females. Thus, whereas viewing appetitive sexual stimuli by males in our current study elicited highly localized increases in amygdala activation, consummatory sexual behavior elicited correspondingly focal deactivations in the amygdala.

Clinical Implications

A number of psychological disorders involving emotional function occur at substantially different rates in men

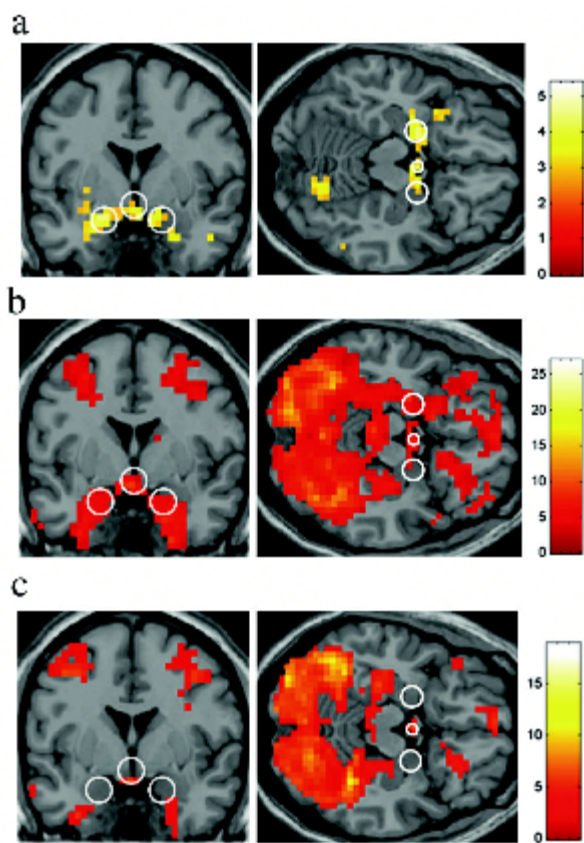


Fig. 3. Results from an fMRI study (Hamann and others 2004) comparing brain responses of men and women to sexually arousing photographs, showing greater activation for men specifically in the bilateral amygdala and the hypothalamus. Brain regions where men showed greater activation than females when viewing sexually arousing photographs versus a control condition in which a fixation cross (+) was presented. The middle circle shows the approximate location of the hypothalamus, whereas the outer two circles indicate the approximate location of the left and right amygdala. Brighter colors on the color bar indicate larger effects (statistical Z scores). The right hemisphere is on the right of the coronal images. (a) *Left:* coronal image showing greater bilateral amygdala and hypothalamic activations for males versus females for the statistical comparison between sexually arousing stimuli and fixation. *Right:* axial view of the same contrast. (b) This shows the more active areas while viewing sexually arousing stimuli versus fixation for the group of men. (c) The same contrast and views for females. In contrast to men, there is a lack of significant activity in the bilateral amygdala and the hypothalamus for women in response to sexually arousing photographs.

versus women. For example, women are about twice as likely in their lifetime to experience clinical depression. Posttraumatic stress disorder (PTSD), an anxiety disorder associated with serious traumatic events and characterized by such symptoms as reliving a trauma in dreams, numbness and lack of involvement with reality, or recurrent thoughts that intrude into daily awareness, also occurs in women about twice as often as in men. Sex differences in the amygdala's response have been cited by several authors as a potentially important factor that may explain why some psychological disorders are

more common in men or women (Davidson and others 2002). Abnormal amygdala function has been observed in depression (Sheline and others 2001), and sex differences in the amygdala's role in emotional memory have been linked to the greater prevalence of depression in women. Specifically, the prevalence of ruminative thinking, the repetitive focusing on negative feelings and memories of negative life experiences, is greater in females than males, and ruminative thinking is also associated with longer and more severe episodes of depression. A consequence of women's tendency to form stronger emotional memories and different patterns of emotion-related amygdala activity may be that memories of negative life events are more available for rumination, contributing to a greater vulnerability to depression. Likewise, current theories of PTSD conceptualize this disorder in terms of basic mechanisms of associative fear conditioning, a nonconscious form of learning involving either an abnormally strong learned fear response to stimuli associated with the trauma that precipitated the disorder or an inability to extinguish (diminish) inappropriate fear responses (Davis and Whalen 2001). Because fear conditioning depends critically on the amygdala, sex differences in amygdala response may partly account for the greater prevalence of PTSD in women.

Turning to disorders more prevalent in men, a number of sexual disorders such as voyeurism are far more prevalent in men (Gomez 1991). The greater amygdala response to visual sexual stimuli and greater appetitive motivation elicited by visual sexual stimuli may contribute to the greater rate of such disorders in males. Lastly, autism, a developmental disability that is characterized by significant deficits in emotion, communication, and social interaction, is approximately four times as common in males than in females. The social and emotional deficits in autism have been speculated to result in part from an altered amygdala function in individuals with autism, partly on the basis of similar deficits that have been observed in patients with lesions to the amygdala (Adolphs and others 1995). The link between the amygdala and autism is further supported by neuroimaging evidence that the amygdala in children with autism undergoes abnormal development (Schumann and others 2004).

Future Directions

Collectively, the findings of these studies support the notion that the amygdala is a key structure mediating differences in emotional behaviors between men and women (see summary in Table 1). As noted previously, the greater prevalence of some psychological disorders may stem in part from sex differences in amygdala responses. The clear clinical implication of this link is that a better understanding of how amygdala function differs between men and women should help shed light on the biological basis for these disorders.

Sex differences in human behavior can arise from multiple causes, including alterations in brain develop-

Table 1. Summary of Patterns of Response in the Left and Right Amygdala for Men and Women Across the Domains of Function Examined in the Studies Reviewed

	Emotional Memory		Emotional Responses (Visual Stimuli)		Emotional Responses (Sexual Stimuli)		Consummatory Sexual Behavior	
	Left	Right	Left	Right	Left	Right	Left	Right
♂	∅	***	***	*	***	**	↓***	∅
♀	***	∅	***	*	∅	∅	∅	∅

In some domains, sex differences take the form of a shift in hemisphere, whereas in other cases the sex difference is primarily manifested in the overall level of amygdala activity. Left and right refer to the left and right amygdala, respectively. Findings are listed on the upper row for males and the lower row for females. Symbol legend: ∅ = activity absent or minimal; * = some significant activity, variable across studies; ** = moderate activity; *** = high activity; ↓ = decreased activity.

ment, differences in brain morphology, the effects of sex hormones, or different social experiences of men and women. Future research will help determine the degree to which each of these factors contributes to sex differences in behavior, as well as the specific role of differences in amygdala response. Neuroimaging studies have only recently started to examine sex differences in emotion and cognition. As more studies begin to examine the neural basis of sex differences in emotion and other domains, a more comprehensive picture of the important similarities and differences between men and women will emerge. For the domain of emotion, the amygdala is likely to feature prominently in this picture.

References

Adolphs R, Tranel D, Damasio H, Damasio AR. 1995. Fear and the human amygdala. *J Neurosci* 15:5879–91.

Arana SF, Parkinson JA, Hinton E, Holland A, Owen AM, Roberts. 2003. Dissociable contributions of the human amygdala and orbitofrontal cortex to incentive motivation and goal selection. *J Neurosci* 23:9632–8.

Baird AD, Wilson SJ, Bladin PF, Saling MM, Reutens DC. 2004. The amygdala and sexual drive: insights from temporal lobe epilepsy surgery. *Ann Neurol* 55:87–96.

Cahill L, Haier RJ, White NS, Fallon J, Kilpatrick L, Lawrence C, and others. 2001. Sex-related difference in amygdala activity during emotionally influenced memory storage. *Neurobiol Learn Mem* 75:1–9.

Cahill L, Uncapher M, Kilpatrick L, Alkire MT, Turner J. 2004. Sex-related hemispheric lateralization of amygdala function in emotionally influenced memory: an fMRI investigation. *Learn Mem* 11:261–6.

Calder AJ, Lawrence AL, Young AW. 2001. Neuropsychology of fear and loathing. *Nat Rev Neurosci* 2:352–63.

Canli T, Desmond JE, Zhao Z, Gabrieli JDE. 2002. Sex differences in the neural basis of emotional memories. *Proc Natl Acad Sci U S A* 99:10789–94.

Canli T, Zhao Z, Brewer J, Gabrieli JDE, Cahill L. 2000. Event-related activation in the human amygdala associates with later memory for individual emotional experience. *J Neurosci* 20:1–5.

Davidson RJ, Pizzagalli D, Nitschke JB, Putnam K. 2002. Depression: perspectives from affective neuroscience. *Ann Rev Psychol* 53:545–74.

Davis M, Whalen PJ. 2001. The amygdala: vigilance and emotion. *Mol Psychiatr* 6:12–34.

Everitt BJ. 1990. Sexual motivation: a neural and behavioral analysis of the mechanisms underlying appetitive and copulatory responses of male rats. *Neurosci Biobehav Rev* 14:217–32.

Goldstein JM, Seidman JL, Horton NJ, Makris N, Kennedy DN, Caviness VS, and others. 2001. Normal sexual dimorphism of the adult human brain assessed by in vivo magnetic resonance imaging. *Cer Ctx* 11:490–7.

Gomez J. 1991. Psychological and psychiatric problems in men. New York: Routledge.

Gottfried JA, O’Doherty J, Dolan RJ. 2003. Encoding predictive reward value in human amygdala and orbitofrontal cortex. *Science* 301:1104–7.

Hamann S. 2001. Cognitive and neural mechanisms of emotional memory. *Trends Cognit Sci* 5:394–400.

Hamann S, Canli T. 2004. Individual differences in emotion processing. *Curr Opin Neurobiol* 14:233–8.

Hamann S, Herman R, Nolan C, Wallen K. 2004. Men and women differ in amygdala response to visual sexual stimuli. *Nat Neurosci* 7:411–6.

Hamann SB, Ely TD, Grafton ST, Kilts CD. 1999. Amygdala activity related to enhanced memory for pleasant and aversive stimuli. *Nat Neurosci* 2:289–93.

Hamann SB, Ely TD, Hoffman JM, Kilts CD. 2002. Ecstasy and agony: activation of the human amygdala in positive and negative emotion. *Psychol Sci* 13:135–41.

Holstege G, Georgiadis JR, Paans AMJ, Meiners LC, van der Graaf HCE, Reinders AATS. 2003. Brain activation during human male ejaculation. *J Neurosci* 23:9185–93.

Karama S, Lecours AR, Leroux J-M, Bourgouin P, Beaudoin G, Joubert S, and others. 2002. Areas of brain activation in males and females during viewing of erotic film excerpts. *Hum Brain Map* 16:1–13.

Leutmezer F, Serles W, Bacher J, Gröppel G, Pataraya E, Aull S, and others. 1999. Genital automatism in complex partial seizures. *Am Acad Neurol* 52:1118.

Newman SW. 1999. The medial extended amygdala 0in male reproductive behavior: a node in the mammalian social behavior network. *Ann NY Acad Sci* 877:242–57.

Schumann C, Hamstra J, Goodlin-Jones BL, Lotspeich LJ, Kwon H, Buonocore MH. 2004. The amygdala is enlarged in children but not adolescents with autism: the hippocampus is enlarged at all ages. *J Neurosci* 24:6392–401.

Seidlitz L, Diener E. 1998. Sex differences in the recall of affective experiences. *J Pers Soc Psychol* 74:262–71.

Sheline YI, Barch DM, Donnelly JM, Ollinger JM, Snyder AZ, Mintun MA. 2001. Increased amygdala response to masked emotional faces in depressed subjects resolves with antidepressant treatment: An fMRI study. *Biol Psychiatr* 50:651–8.

Squire LR, Zola SM. 1996. Structure and function of declarative and nondeclarative memory systems. *Proc Natl Acad Sci U S A* 93:13515–22.

Strange BA, Hurlmann R, Dolan RJ. 2003. An emotion-induced retrograde amnesia in humans is amygdala- and beta-adrenergic dependent. *Proc Natl Acad Sci U S A* 100:13626–31.

Symons D. 1979. The evolution of human sexuality. Oxford, UK: Oxford University Press.